

LONG-LASTING SUBSTRATE MARKING IN THE COLLECTIVE HOMING OF THE GASTROPOD *NERITA TEXTILIS*

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ABSTRACT

Field observations and experiments were conducted on the intertidal gastropod *Nerita textilis* Gmelin along the Somalian coast to determine if its rhythmical mass-homing includes the detection of durable substrate marking as well as short-term trail-following. The snails' first response to displacement is a zonal orientation compensating for the vertical component of experimental shifting. The homing performance of symmetrically transferred animals supports the hypothesis that a marked area is present in and below the aggregation site, detectable by the homer snails 24 hours after its deposition by spontaneously moving conspecifics. No specific marking of different collective homes resulted from these experiments.

INTRODUCTION

Experimental evidence shows the importance of trail-following in the orientation of molluscs toward goals of different ecological significance, including rest sites (Newell, 1979; Underwood, 1979). The Indo-Pacific intertidal gastropod *Nerita textilis* Gmelin performs looped feeding excursions whose homeward branch partly overlaps its outward path. Moreover, arena tests show inter-individual short-term retracing as well (Chelazzi *et al.*, 1983). Under high population density this species shows markedly rhythmical clustering during all high tides and low tides occurring between about midnight and noon (Vannini and Chelazzi, 1978). This rhythmical aggregation is controlled by external (tidal) factors and spatial interactions between members of the population (Chelazzi *et al.*, 1984).

Collective homing of *N. textilis* and other gregarious intertidal gastropods (Moulton, 1962; Magnus and Haacker, 1968; Willoughby, 1973) would seem to require not only a capacity to follow freshly deposited mucous trails but also the ability to detect long-lasting chemical cues, including a durable system of trails connecting feeding and resting places, as well as the marking of collective homes. The capacity to follow durable mucous trails and the use of stable chemical labeling of the rest site are both present in some solitary-homer intertidal gastropods (Funke, 1968; Cook, 1969).

The displacement experiments reported in this paper were designed to verify if *N. textilis* homes not only through the use of short-term trail-following, but also by detection of long-lasting chemical cues.

MATERIALS AND METHODS

Experiments and observations were conducted at different sites along the Benadir coast (Somalia), whose morphology and intertidal ecology have been described elsewhere (Chelazzi and Vannini, 1980a). Observations on natural behavior were performed using photography at set intervals.

Received 12 May 1984; accepted 18 January 1985.

Tides are semidiurnal along the Somalian coast and during the test period (around spring tide) low tides occurred at about 11:00 and 23:00 h. Displacement tests were performed by collecting all snails resting in each cluster during the morning (08:00–11:00), marking them individually by a number-color code, and transferring them immediately to the release point. Their position was recorded 24 h later at the following diurnal low tide. Since *N. textilis* moves only once a day (for about 7 h) during afternoon and night low tides (Vannini and Chelazzi, 1978), the time between displacement and recording comprised only one activity phase.

For the *single-cluster* tests a total of 140 snails resting in three aggregations were divided into four groups of equal size ($n = 35$) and released from points 150 cm above, below, to the left, and to the right of their original cluster. Their position with respect to the release site was recorded 24 h later. Moreover, an additional 403 snails were transferred as above from 6 aggregations; the number of those returned to their original cluster was recorded 24 h later.

The *crossing* tests consisted of collecting all snails resting in twin clusters 160–200 cm apart at the same shore level. Members of left and right clusters were divided into two lots of almost equal size and transferred below each original cluster or obliquely, below the side cluster. The number of displaced snails returned to each cluster was recorded 24 h later. Three replicates of the experiment were performed on different cluster couples, for a total of 133 vertically and 138 obliquely transferred snails.

Circular distributions of recovery directions (*single-cluster* test) were analyzed according to current circular statistics (Batschelet, 1981).

RESULTS

Field observations

Photographs taken during clustering and disaggregation show evidence of interaction between moving snails. During their return from the feeding zone the snails either form pre-aggregation clumps which move compactly to the sheltered areas (fast return under strong wave movement) or sparsely follow a web of trails (slow return under moderate wave action). Mucous trails are evident under the latter circumstances and the web progressively clumps into a few major trails leading to the cluster site (Fig. 1). Snails follow the trail system singly or in small groups. Moreover, queuing is commonly observed during the early downward migration following disaggregation (Fig. 2).

Besides the web of trails traced on the shore during migration, rest places also show distinct long-lasting features: where clusters usually form, the rocky wall differs in color from the neighboring zones. Moreover, cluster sites are constant not only day after day but also after their periodic vacancy during the synodic month (Chelazzi *et al.*, 1984). The long-lasting marking of rest areas is also suggested by the return rate of snails to temporarily abandoned clusters. In most cases this phenomenon appears suddenly: at the first rest phase of occupancy the mean number of aggregating snails is about 72% of the saturation size of each cluster.

Experimental displacement

Inspection of the shore during the 24 h period between displacement and position-recording confirmed that throughout the test period transferred snails moved only during the nocturnal low tide. The angular distributions obtained from the *single-cluster* tests show that the snails adjusted zonally to displacement. When

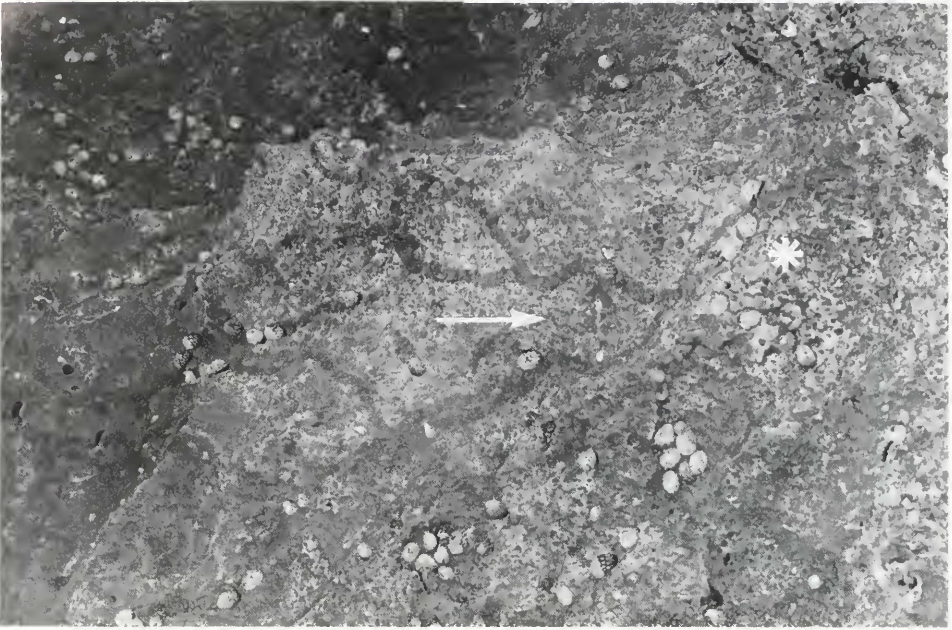


FIGURE 1. Night photograph of the shore during early cluster formation, showing a web of mucous trails leading to a cluster area (asterisk). Snails returning from their feeding excursions following trails are visible (arrow: direction of movement). Sea is at the left.



FIGURE 2. Afternoon photograph of the same stretch of shore as in Figure 1, during early downward movement (arrow) from the cluster area (asterisk).

released above (Fig. 3A) and below (Fig. 3B) their original site they headed respectively downwards and upwards (V test, $P < 0.01$ for both distributions). The two distributions differ statistically from each other according to Watson's U^2 test ($U^2_{25,31} = 1.06$; $P < 0.01$). The lateral displacements (Fig. 3C-D) were followed by bimodal heading distributions (Rao's test, $P < 0.01$) since the snails moved in both horizontal directions after release. The two distributions are not statistically different ($U^2_{29,34} = 0.09$; $P > 0.10$), but the cumulative distribution of headings after lateral displacements differs statistically from that obtained after upwards ($U^2_{25,63} = 0.65$; $P < 0.01$) and downwards ($U^2_{31,63} = 0.96$; $P < 0.01$) releases.

The number of snails which returned to their original cluster site differs between the various release sites (Fig. 4). Homing performance was significantly higher following downward rather than upward ($\chi^2 = 23.99$; $P < 0.01$) or horizontal displacement ($\chi^2 = 25.91$; $P < 0.01$). The return from release sites above the cluster area was slightly lower than from the lateral places, but the difference was not statistically significant in the present sample size ($\chi^2 = 0.91$; $P > 0.05$).

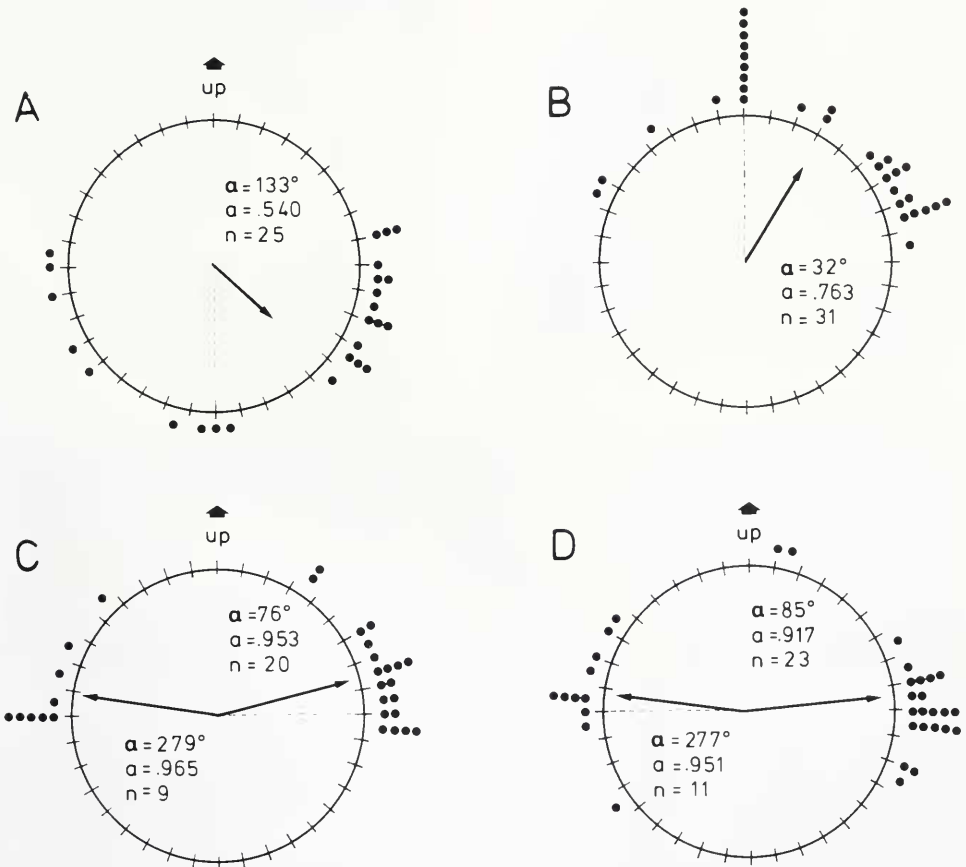


FIGURE 3. Headings of snails after displacement above (A), below (B), to the left (C), and to the right (D) of their cluster site. Inner dashed line: original home direction; inner arrow: mean vector. The polar coordinates and sample size of each distribution are also shown. C and D distributions were analyzed as bimodal (rightward and leftward) distributions.

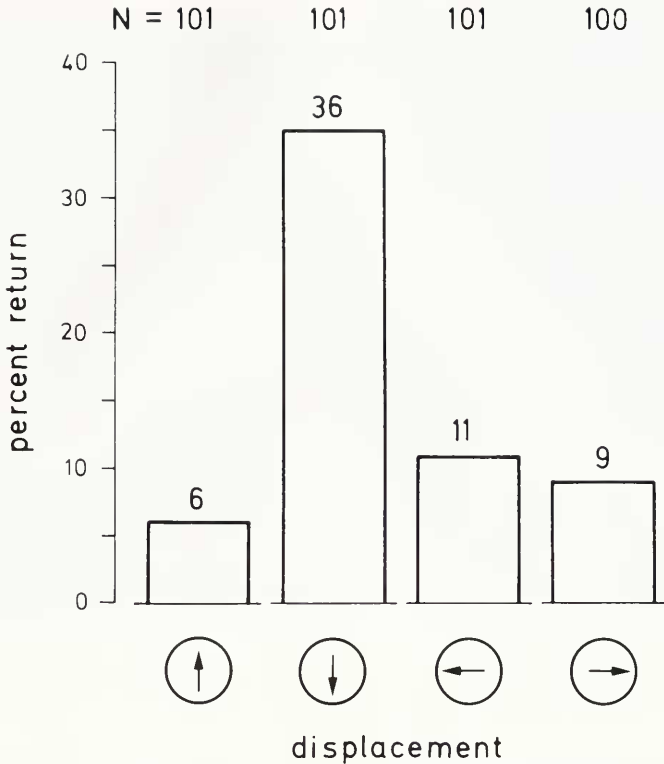


FIGURE 4. Homing performance relative to the *single-cluster* test, expressed as percent of the number displaced in each direction (N). Number of animals recovered in their original cluster after each displacement is shown above each histogram.

The majority of the non-homed snails were either lost—probably dislodged by waves during high tide (about 15%)—or remained scattered, while a fraction was observed in adjacent clusters. *Crossing* tests were performed in order to quantify the change of cluster after displacement and to verify if snails significantly preferred their original aggregation. Out of a total of 144 snails recovered in both test clusters, 68 were found in the cluster above the release site (47.2%) and 76 to the side ($\chi^2 = 0.57$; $P > 0.05$). Figure 5 shows no evidence for a preference of original *versus* adjacent aggregation ($\chi^2 = 0.37$; $P > 0.05$).

DISCUSSION

The first response of *Nerita textilis* specimens, after being transferred from their cluster sites, is a compensation for the vertical component of experimental displacement. Long-distance (10–50 m) seaward displacement of this species, and the congeneric *N. plicata*, has revealed this compensative zonal orientation (Chelazzi and Vannini, 1976; 1980b) which has also been demonstrated in *Littorina irrorata* (Hamilton, 1978), *L. littorea* (Gowanloch and Hayes, 1926; Gendron, 1977), and *L. punctata* (Evans, 1961). But the present study revealed a very precise and fast zonal adjustment.

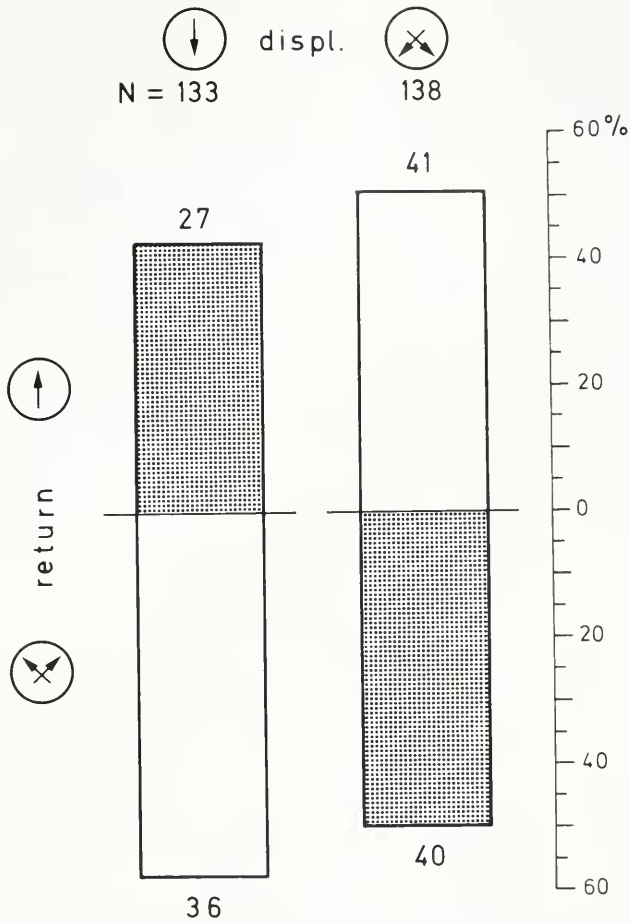


FIGURE 5. Homing performance relative to the *crossing* tests: upward (above) and diagonal (below) return, expressed as percent of snails recovered after downward (left) and oblique (right) displacement. Total numbers of displaced snails are shown above the histograms (N). Shaded histograms: snails returned to the original cluster.

Among the probable factors informing the animals about their vertical shift are the variation of exposure to waves during high tide and physical substrate conditions (hydration and temperature) during low tide. These cues could trigger a directional orientation such as geotaxis, following the complex integration between releasing and orienting mechanisms frequently involved in the zonal orientation of intertidal gastropods (Fraenkel, 1927; Kristensen, 1965; Bock and Johnson, 1967; Bingham, 1972; Underwood, 1972a, b; Chelazzi and Focardi, 1982).

However, alone this precisely tuned zonal behavior cannot guarantee the relocation of a spatially definite goal such as the aggregation area, 10–40 cm in diameter. An additional stopping effect on moving animals based on long-lasting marking of the cluster area could explain some aspects of the natural mass-homing of *N. textilis*, including the sudden occupancy of aggregation sites and their long-term spatial stability. Nonetheless, the difference in the homing performance

recorded from four symmetrical release sites supports the hypothesis that the marked area extends downward from the aggregation site and is probably arranged in a roughly triangular shape with its vertex in the cluster area and the base downward. This could explain the significantly higher homing performance after downward displacement with respect to upward and lateral transfer.

A channeling effect due to shore morphology (crevices, etc.) can be ruled out in these experiments as the rock surface around the test clusters showed no special features. *N. textilis* generally congregates either in tide-pools of various shapes or on flat areas (Chelazzi *et al.*, 1984). While collective homing could be facilitated by drainage channels spreading down from the pools, the frequent clustering on flat surfaces must be based on factors not related to cliff morphology. Moreover, even when clustering in tide-pools, snails do not randomly use every site suitable for resting but congregate in a few areas which greatly resemble the unfrequented sites.

Chemical marking is evidently produced by the repeated release of mucus as the snails migrate downward and up the cliff during their natural feeding excursions (Chelazzi *et al.*, 1983). The experimental procedure, involving the complete destruction of original clusters during a rest phase and the control of homing 24 h later, excluded the possibility that homing of displaced animals was based on freshly lain trails; the marked area had an age of at least one day under present test conditions.

These conclusions do not contradict the available laboratory information on the survival of orienting cues in the trails of other gastropods. While in the freshwater snails *Biomphalaria glabrata* (Townsend, 1974; Bousfield *et al.*, 1981) and *Physa acuta* (Wells and Buckley, 1972) or periwinkles *Littorina planaxis* (Raftery, 1983) and *L. littorea* (Gilly and Swenson, 1978) the directional information contained in the trail seems to be significantly retained only shortly after deposition (10–30 min), other species produce long-lasting trails whose detectability by conspecifics ranges from 4 h in the mud snail *Ilyanassa obsoleta* (= *Nassarius obsoletus*) (Trott and Dimock, 1978) to one or two days in the pulmonate limpets *Siphonaria normalis* and *S. alternata* (Cook, 1969, 1971). Longer trail survival was found in the terrestrial slug *Limax grossii* (= *L. pseudoflavus*) (Cook, 1976).

Laboratory tests show that *N. textilis* recognizes the direction of freshly lain trails (Chelazzi *et al.*, 1983), but its clustering in the field does not necessarily require intrinsic trail-polarization since collective homing is performed by this species on vertical rocky cliffs where the correct (homeward) following could be based on such external cues as gravity.

Finally, no evidence emerged from our tests about the informational difference between trail-webs spreading out from various clusters, which agree with the usually observed inter-cluster turnover in the collective homing of *N. textilis* (Chelazzi *et al.*, 1984) and other gregarious gastropods (Moulton, 1962; Willoughby, 1973).

ACKNOWLEDGMENTS

This work was supported by the Centro di Studio per la Faunistica ed Ecologia Tropicali del Consiglio Nazionale delle Ricerche. We are grateful to Prof. L. Pardi and Prof. A. Ercolini for their advice and criticism.

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